CHAPTER 8:
PATTERNS OF PLANT DIVERSITY

RESULTS

Patterns of Plant Alpha Diversity

General Patterns

I detected a total of 470 native species and 224 native plant genera. Plant species richness varied from 33 to 133 species per reach ($\bar{x}$ = 71.2, SE = 2.05). Only 11 species occurred on over 75% of all sample reaches (Fig. 51), and they accounted for 13% of all observations.
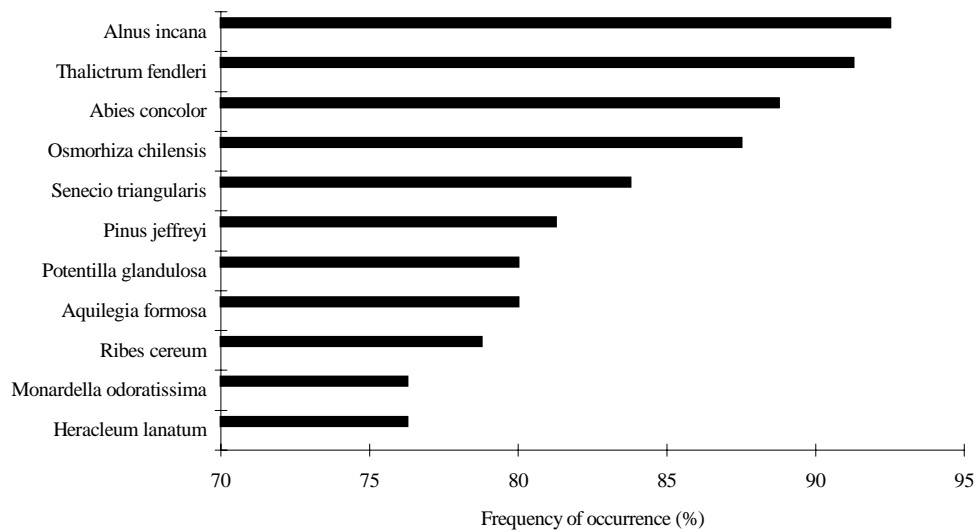

FIG. 51. Plant species occurring on > 75% of all sample reaches. Data were collected on sample reaches (*n* = 80) in the Lake Tahoe basin, 1995 to 1996.

Environmental Relationships of Plant Richness
Regression Model for Plant Richness

Species richness was strongly correlated with 4 physical variables: significant positive correlations with precipitation, channel width, and east aspects, and negative correlations with west aspects (Table 129). Species richness was also significantly correlated with 4 vegetation variables: positively correlated with lodgepole pine, and small and large logs; and a negative correlation with meadow (Table 129).

TABLE 129. Significant correlations ($P \leq 0.10$) between plant species and 22 environmental variables. Bolded values indicate $P \leq 0.05$. Data were collected on sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996.

	Plant species richness	
Environmental variable	r	P
Abiotic environment:		
Precipitation	**0.341**	**0.002**
East aspect	**0.246**	**0.028**
West aspect	**-0.322**	**0.004**
Channel characteristics:		
Width	**0.233**	**0.038**
Vegetation characteristics:		
Lodgepole pine	**0.238**	**0.033**
Meadow	**-0.248**	**0.027**
Small log	**0.245**	**0.028**
Large log	0.195	0.083

Regression results for plant species richness reflected correlations (Table 130). Regression on abiotic environmental variables resulted in a 2-variable model: a positive association with precipitation and a negative association with west aspects (adj. $R^2 = 0.142$). Regression on channel characteristics resulted in a weak one-variable model: a positive association with width (adj. $R^2 = 0.042$). Regression on vegetation characteristics resulted in a 4-variable model: a positive association with aspen–cottonwood, subalpine conifer, and lodgepole pine, and negative associations with meadow (adj. $R^2 = 0.191$). The final backwards regression on these 7 key variables resulted in a 3-variable model, where plant species richness increased with increases in aspen–cottonwood, lodgepole pine, and precipitation, and decreases in meadow (adj. $R^2 = 0.217$) (Tables 130 and 131).

TABLE 130. Variables selected in step-wise regressions for plant species richness and 3 groups of environmental variables ($n = 22$). N = negative association and P = positive association at $P \leq 0.10$. Bolded = selected in the final regression at $P \leq 0.05$ on key variables from each group of environmental variables. Data were collected on sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996.

Environmental variable	Plant species richness
Abiotic environment:	
Precipitation	**P**
West aspect	N
Channel characteristics:	
Width	P
Vegetation characteristics:	
Lodgepole pine	**P**
Subalpine conifer	P
Aspen−cottonwood	**P**
Meadow	**N**
Variables in final model	*4*
adj. R^2	*0.217*

TABLE 131. Final backwards regression model for plant species richness relative to environmental variables. Data were collected at sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996. Beta = partial regression coefficient.

Environmental variables	B	SE of B	Beta	T	*P*
Precipitation	16.12	5.779	0.295	2.789	0.007
Meadow	-17.29	6.299	-0.288	-2.745	0.008
Lodgepole pine	16.53	6.364	0.275	2.597	0.011
Aspen−cottonwood	26.34	12.287	0.222	2.143	0.035

I looked for potential thresholds in species richness in relation to the 4 environmental variables selected in the final regression models. Where lodgepole pine was over 10% of the reach, plant species richness was at least 50 species, and plant species richness was significantly greater where lodgepole pine exceeded 10% of the reach (1-tailed test, pooled variance, t = 2.24, P = 0.018). Plant species richness appeared to peak when lodgepole pine occupied approximately 40% of the reach area, indicating a slightly curvilinear relationship between plant species richness and lodgepole pine (Fig. 52). Additionally, plant species richness was consistently above 60 species when aspen−cottonwood was $\geq$ 10% of the reach area, whereas reaches with < 10% aspen cottonwood species richness dropped as low as 30 (Fig. 53). However, plant species richness was not significantly greater where aspen–cottonwood exceeded 10% (1-tailed test, pooled variance, P = 0.357). Finally, plant species richness appeared to have a curvilinear relationship with precipitation, where richness peaked at intermediate levels of precipitation (110 to 130 cm/yr) (Fig. 54).
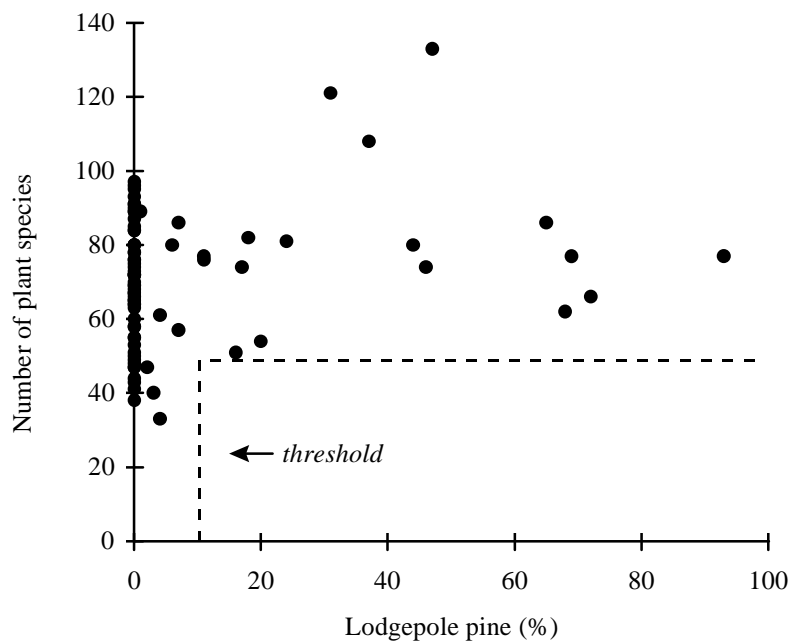
FIG. 52. Threshold between lodgepole pine and plant species richness in sample reaches (*n* = 80) in the Lake Tahoe basin, 1995 to 1996.
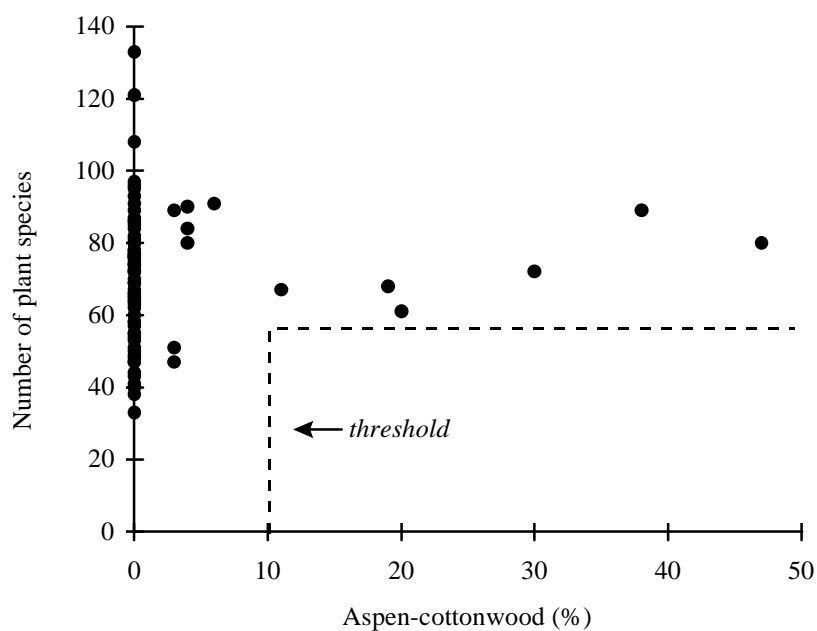

FIG. 53. Threshold between aspen−cottonwood and plant species richness in sample reaches (*n* = 80) in the Lake Tahoe basin, 1995 to 1996.
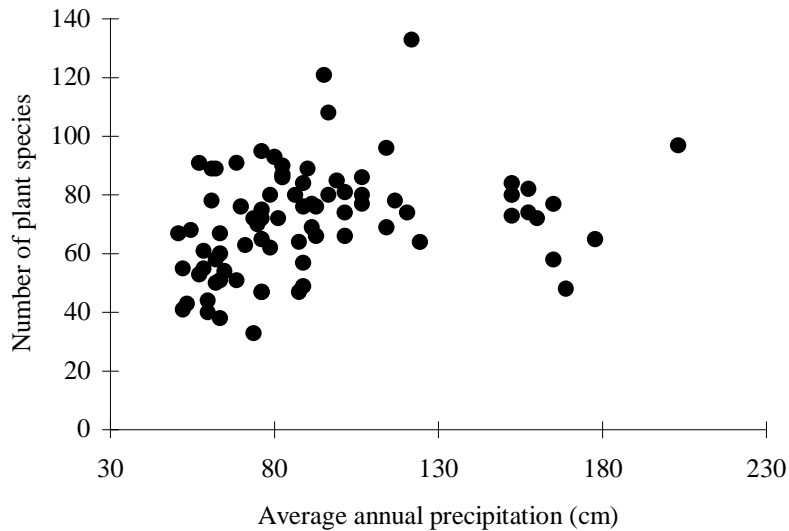
FIG. 54. Threshold between precipitation and plant species richness in sample reaches ($n =$ 80) in the Lake Tahoe basin, 1995 to 1996.

A quadratic regression between precipitation and plant species richness resulted in a stronger, but less significant regression model (adj. $R^2 = 0.162$, B = 365.08, SE of B = 137.90, Beta = 6.67, T = 2.647, $P = 0.010$) compared to linear regression (adj. $R^2 = 0.105$, B = 18.62, SE of B = 5.82, Beta = 0.34, T = 3.198, $P = 0.002$).

Plant Species Richness by Environmental Gradients

Plant species richness showed few correlations with the 7 relevant environmental gradients (channel log volume not included) defined by PCA (see Environmental Characteristics section above) (Table 132). Plant species richness was positively correlated with the elevation−precipitation, alder−willow, and snag and log gradients.

Plant Richness by Basin Orientation

Plant species varied significantly by basin orientation. Plant species richness was greater on the west and north sides compared to the east side of the basin ($v = 3$, 76; SS = 5481.02, 21,105.17; MS = 1827.01, 277.70; F = 6.58, $P < 0.001$). The west side had significantly greater precipitation, channel widths, and subalpine conifer compared to the east side, and the east side had a significantly greater amount of mixed conifer compared to the west side of the basin (see Chapter 4).

TABLE 132. Significant ($P \leq 0.10$) correlations between plant species richness and 7 environmental gradients, as defined by principal components analysis. Bolded values indicate $P \leq 0.05$. N and P indicate non-significant (n.s.) negative and positive correlations, respectively. Data were collected on sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996.

Environmental gradient	Plant species richness	
	r	*P*
Physical gradient:		
1. Elevation−precipitation	**0.240**	**0.032**
2. Channel flow	0.155	0.171
Vegetation gradient:		
1. Forest to meadow	0.007	0.949
2. Subalpine vegetation	-0.002	0.989
3. Alder−willow	**0.284**	**0.011**
4. Aspen−cottonwood	-0.110	0.334
Woody debris gradient:		
1. Snag and log	**0.232**	**0.038**

Patterns of Plant Alpha Diversity by Habitat Association

General Patterns

Approximately 45% ($n = 213$) of all plant species observed were determined to be aquatic−riparian−meadow associates (as opposed to upland associates). At least 5 aquatic−riparian−meadow plant species occurred on each reach, with the average number of aquatic−riparian−meadow plants being 32.3 species per reach (Table 133). A minimum of 8 upland-associated plant species were observed on every reach, with an average of 38.9 species per reach (Table 129).

TABLE 133. Descriptive statistics for the richness of 2 plant species groups based on habitat associations. Data were collected at sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996.

Plant groups	Total species possible	Min.	Max.	Ave.	SE
Aquatic−riparian−meadow-associated	213	5	77	32.3	1.29
Upland-associated	257	8	58	38.9	1.24

The contribution of individual species to the richness values for each group varied based on the relative frequency of the species. The 10 most frequently occurring aquatic−riparian−meadow-associated species were present on over 66% of the reaches, with 4 species occurring on over 80% of the reaches: *Alnus tenuifolia* (mountain alder), *Senecio triangularis* (arrowleaf groundsel), *Potentilla glandulosa* (sticky cinquefoil), and *Aquilegia formosa* (crimson columbine) (Fig. 55). The 10 most frequently occurring upland-associated species were present on over 67% of the reaches with 4 species occurring on over 80% of the reaches: *Thalictrum fendleri* (Fendler's meadow rue), *Abies concolor*, *Osmorhiza chilensis* (mountain sweet cicily), and *Pinus jeffreyi* (Fig. 56).
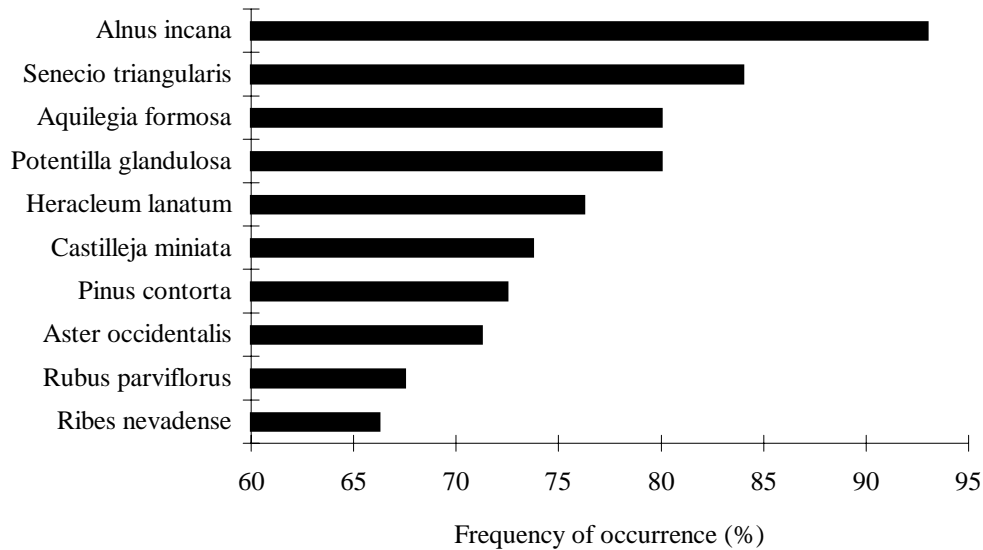

FIG. 55. Ten most frequently occurring aquatic−riparian−meadow-associated plant species in sample reaches (*n* = 80) in the Lake Tahoe basin, 1995 to 1996.
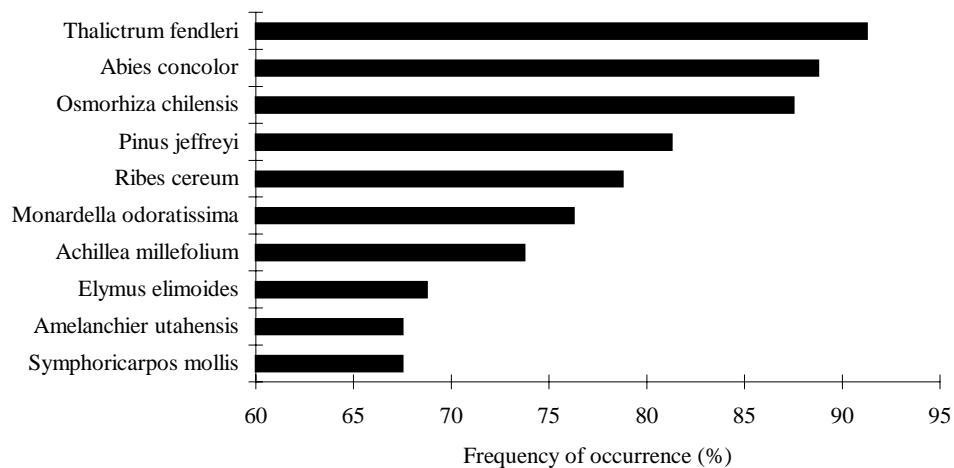

FIG. 56. Ten most frequently occurring upland-associated plant species in sample reaches (*n* = 80) in the Lake Tahoe basin, 1995 to 1996.

Environmental Relationships of Plant Groups
Correlations

Aquatic−riparian−meadow associates and upland associates both had significant relationships with 2 environmental variables: mixed conifer and channel gradient (Table 134). Aquatic−riparian−meadow plant richness was negatively correlated with mixed conifer and channel gradient, whereas upland plant richness was positively correlated with these two variables. Aquatic−riparian−meadow plant richness was negatively correlated with gradient and mixed conifer, whereas upland plant richness was positively correlated with both variables. Aquatic−riparian−meadow plant richness was correlated with an additional 8 variables: positive correlations with precipitation, east aspects, channel width, alder−willow and lodgepole pine; and negative correlations with canopy cover density and shrubs (Table 134). Upland plant richness was correlated with an additional 5 variables: positive correlations with large and small logs, and large and small snags; and a negative correlation with meadow (Table 134).

Regression Model for Aquatic−riparian−meadow-associated Plant Richness

Regression of aquatic−riparian−meadow associate richness on abiotic environmental variables resulted in a 2-variable model: positive association with precipitation and a negative association with west aspects (adj. R^2= 0.179) (Table 135). Regression on channel variables resulted in a 2-variable model: a positive association with width and a negative association with gradient (adj. R^2 = 0.170). Regression on vegetation variables resulted in a 4-variable model: positive associations with aspen−cottonwood, alder−willow, subalpine conifer, and lodgepole pine (adj. R^2 = 0.313). Backwards step-wise regression on these 8 key variables resulted in a 4-variable model, where richness of aquatic−riparian−meadow species increased with increases in precipitation, aspen−cottonwood, alder−willow and lodgepole pine (adj. R^2 = 0.363) (Tables 135 and 136).

TABLE 134. Significant correlations ($P \le 0.10$) between species richness for 2 plant groups (aquatic−riparian−meadow and upland) and 22 environmental variables. Bolded values indicate $P \le 0.05$. N and P indicate non-significant (n.s.) negative and positive correlations, respectively. Data were collected on sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996.

| | Plant species group | | | |
| | Aquatic−riparian−meadow associates | | Upland associates | |
Environmental variable	r	*P*	r	*P*
Abiotic environment:				
Precipitation	**0.394**	**<0.001**	P	n.s.
East aspect	**0.254**	**0.023**	P	n.s.
West aspect	**-0.335**	**0.002**	N	n.s.
Channel characteristics:				
Gradient	**-0.385**	**<0.001**	**0.255**	**0.023**
Width	**0.320**	**0.004**	P	n.s.
Sinuosity	P	n.s.	**-0.251**	**0.025**
Vegetation characteristics:				
Mixed conifer	**-0.394**	**<0.001**	0.188	0.094
Alder−willow	**0.262**	**0.019**	P	n.s.
Lodgepole pine	**0.469**	**<0.001**	N	n.s.
Meadow	P	n.s.	**-0.528**	**<0.001**
Shrub	**-0.225**	**0.045**	P	n.s.
Canopy cover index	**-0.351**	**0.001**	P	n.s.
Small log	P	n.s.	**0.360**	**0.001**
Large log	N	n.s.	**0.384**	**<0.001**
Small snag	P	n.s.	**0.261**	**0.019**
Large snag	N	n.s.	**0.236**	**0.035**

I looked for potential thresholds in aquatic−riparian−meadow-associated plant species richness in relation to the 4 variables selected in the final regression model. Aquatic−riparian−meadow plant species richness had a curvilinear relationship with precipitation that was almost identical to that observed for the richness of all plant species, with the peak in richness occurring at intermediate precipitation values (Fig. 57). Upland plant species richness did not show any relationship with precipitation. The presence of aspen−cottonwood was always associated with the presence of 20 or more aquatic−riparian−meadow plant species; however, upland plant species richness was not significantly greater in the presence of aspen-cottonwood (1-tailed test, pooled variance, $P = 0.108$).

TABLE 135. Variables selected in step-wise regressions between 3 groups of environmental variables ($n = 22$) and species richness for 2 plant groups. N = negative association and P = positive association at $P \leq 0.10$. Bolded = selected in the final regression at $P \leq 0.05$ on key variables from each group of environmental variables. Data were collected on sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996.

	Plant habitat group	
Environmental variable	Aquatic−riparian−meadow associates	Upland associates
Abiotic environment:		
Precipitation	**P**	-
West aspect	N	-
Channel characteristics:		
Gradient	N	P
Width	P	-
Vegetation characteristics:		
Alder−willow	**P**	-
Aspen−cottonwood	**P**	-
Subalpine conifer	P	-
Lodgepole pine	**P**	-
Meadow	-	**N**
Variables in final model	*4*	*1*
adj. R^2	*0.363*	*0.267*

TABLE 136. Final linear regression model of key environmental variables in relation to species richness of 2 plant species groups (aquatic−riparian−meadow and upland associates). Data were collected on sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996. Beta = partial regression coefficient.

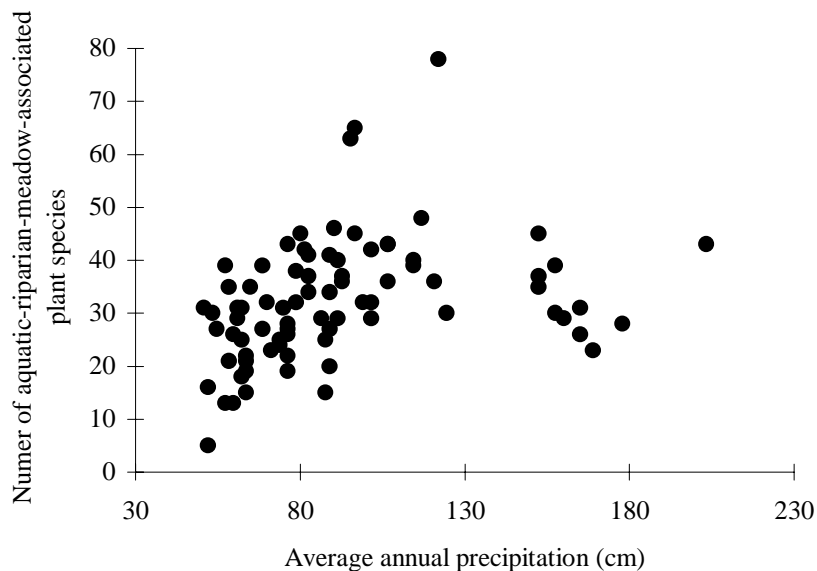| Variable	B	SE of B	Beta	T	*P*
Aquatic−riparian−meadow-associates:					
Precipitation	12.032	3.221	0.351	3.735	< 0.001
Aspen/cottonwood	17.198	6.912	0.231	2.488	0.015
Lodgepole pine	15.304	3.494	0.407	4.380	< 0.001
Alder/willow	10.900	5.801	0.171	1.879	0.064
Upland−associates:					
Meadow	-19.198	3.494	-0.528	-5.495	<0.001

FIG. 57. Threshold between precipitation and the richness of aquatic−riparian−meadow plant species in sample reaches (*n* = 80) in the Lake Tahoe basin, 1995 to 1996.

Regression Model for Upland-associated Plant Richness

Regression of upland-associate richness on abiotic environmental variables resulted in no variables being selected (Table 135). Regression on channel variables resulted in a one-variable model: a positive association with channel gradient (adj. R^2 = 0.053). Regression on vegetation variables resulted in a one-variable model: a negative association with meadow (adj. R^2 = 0.270). Backwards step-wise regression on these 2 key variables resulted in a one-variable model, where the richness of upland−associated plant species increased with increases in meadow (adj. R^2 = 0.267) (Tables 135 and 136). I looked for potential thresholds in upland-associated plant species richness in relation to meadow, but no threshold was evident.

Plant Groups by Environmental Gradients

Numerous significant correlations were observed between the richness of plant groups and environmental gradients (Table 137). Aquatic−riparian−meadow species richness was positively correlated with both elevation−precipitation and channel flow, whereas upland species richness was not significantly correlated with either physical gradient (Table 137).
Aquatic−riparian−meadow richness and upland richness had opposing relationships with the forest to meadow gradient, with aquatic−riparian−meadow species richness being positively correlated and upland species richness being negatively correlated (Table 137).
Aquatic−riparian−meadow species richness was also positively correlated with alder−willow. Upland species richness was positively correlated with the snag and log gradient and negatively correlated with the forest to meadow gradient (Table 137).

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TABLE 137. Significant ($P \le 0.10$) correlations between plant habitat group variables and principal component analysis factors. Bolded values indicate $P \le 0.05$. r = correlation coefficients. N and P indicate non-significant (n.s.) negative and positive correlations, respectively. Data were collected at sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996.

| | Plant species group | | | |
| | Aquatic−riparian−meadow associates | | Upland associates | |
Environmental gradient	r	*P*	r	*P*
Physical gradient:				
1. Elevation−precipitation	0.206	0.067	0.184	0.104
2. Channel flow	**0.412**	**<0.001**	-0.172	0.128
Vegetation gradient:				
1. Forest to meadow	**0.391**	**<0.001**	**-0.392**	**<0.001**
2. Subalpine vegetation	-0.105	0.354	0.106	0.349
3. Alder−willow	**0.339**	**0.002**	0.119	0.294
4. Aspen−cottonwood	-0.078	0.493	-0.101	0.375
Woody debris gradient:				
1. Snag and log	-0.030	0.793	**0.414**	**<0.001**

Plant Groups by Basin Orientation

Species richness of both plant groups differed by basin orientation. The richness of aquatic−riparian−meadow plant species was significantly greater on the west side of the basin compared to the east and north sides ($v = 3, 76$; SS = 3024.38, 7413.11; MS = 1008.13, 97.54; F = 10.34; $P < 0.001$). Aquatic−riparian−meadow plant species richness generally followed a precipitation cline, being greatest on the west side, followed by the south, then north, and finally was lowest on the east side.

The richness of upland plant species was greater on the north side of the basin compared to the east side ($v = 3, 76$; SS = 995.84, 8735.71; MS = 331.95, 114.94; F = 2.888; $P = 0.041$). Richness was highest on the north side, followed by the west, then south, and was lowest on the east side of the basin.

Patterns of Plant Rarity

General Patterns

Almost 80% of all plant species occurred on less than 25% of sample reaches (Fig. 58). The number of plant species with frequency of occurrence < 10% totaled 290 species (62% of all species), whereas plant species with ≥ 10% totaled 180 species (38%). The number of rare species per reach ranged from 0 to 34 species, and common species ranged from 27 to 102 species per reach (Table 138). The number of rare plant species was highly correlated ($P < 0.001$) with percent rare and percent common species. As a result, only the number of rare and common plant species were used for further analysis.
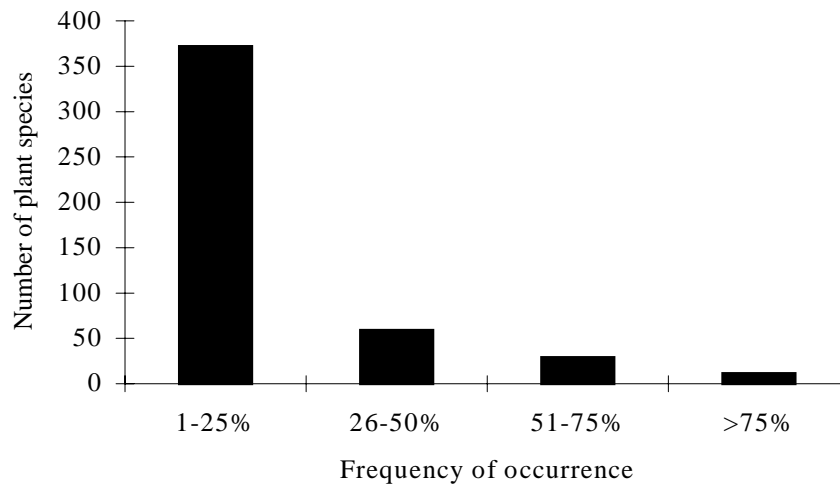
FIG. 58. Number of plant species occurring in each of 4 frequency of occurrence intervals. Data were collected on sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996.

TABLE 138. Descriptive statistics for measures of frequency class variables. Data were collected on sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996.

Frequency class variable	Minimum	Maximum	Average	SE
Number of rare species	0	34	8.5	0.66
Number of common species	27	102	62.7	1.73
% rare species	0	30.0	12.0	1.00
% common species	70.0	100.0	88.0	1.00

Environmental Relationships of Plant Rarity
Correlations

The frequency class variables were correlated with the 22 environmental variables, and a number of significant correlations were observed (Table 139). The number of rare species and common species were both positively correlated with precipitation, and had opposite correlations with large logs and meadow, where rare species were negatively correlated with large snags and positively correlated with meadow. In addition to these shared variables, the number of rare species was positively correlated with channel width and lodgepole pine, and negatively correlated with channel gradient, canopy cover index, south aspects, and mixed conifer. The number of common species was additionally positively correlated with east aspects, small logs, large logs, and alder willow, and negatively correlated with west aspects.

TABLE 139. Significant ($P \leq 0.10$) correlations between plant species frequency class variables and environmental gradients, as defined by principal components analysis. Bolded values indicate $P \leq 0.05$. N and P indicate non-significant (n.s.) negative and positive correlations, respectively. Data were collected on sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996.

| | Plant frequency classes | | | |
| | Number of rare species | | Number of common species | |
Environmental variables	r	*P*	r	*P*
Abiotic environment:				
Precipitation	**0.223**	**0.047**	**0.318**	**0.004**
East aspect	P	n.s.	**0.229**	**0.041**
West aspect	N	n.s.	**-0.331**	**0.003**
South aspect	**-0.230**	**0.041**	N	n.s.
Channel characteristics:				
Gradient	**-0.390**	**<0.001**	P	n.s.
Width	**0.331**	**0.003**	P	n.s.
Vegetation characteristics:				
Mixed conifer	**-0.327**	**0.001**	N	n.s.
Alder−willow	N	n.s.	0.211	0.060
Meadow	0.189	0.093	**-0.366**	**0.001**
Subalpine vegetation	P	n.s.	0.190	0.091
Lodgepole pine	**0.374**	**0.001**	P	n.s.
Canopy cover index	**-0.437**	**<0.001**	N	n.s.
Large snag	**-0.231**	**0.039**	0.186	0.098
Small snag	N	n.s.	**0.241**	**0.031**
Large log	N	n.s.	**0.327**	**0.003**
Small logs	N	n.s.	**0.343**	**0.002**

The number of rare and common species indicated opposing relationships for 4 variables (Table 139). In addition to large logs and meadow mentioned above, rare and common species showed non-significant opposing relationships for gradient, small and large logs, small snags, and alder−willow. Although not significant, these opposing relationships provide some additional evidence that relative to commons species, rare species are associated with more open, flat environments with less developed riparian vegetation.

Regression Model for Rare Plant Species Richness

Individual regression models for the number of rare plant species compared to each of the 3 environmental variable groups resulted in a 2-variable model for abiotic environment (a positive association with precipitation and a negative association with south aspects; adj. $R^2 = 0.072$), a 2-variable model for channel characteristics (a positive association with width and negative association with gradient; adj. $R^2 = 0.177$), and a 3-variable model for vegetation characteristics (positive association with lodgepole pine, and negative associations with canopy cover index and large logs; adj. $R^2 = 0.251$) (Table 140). Backwards step-wise regression on these 7 key variables resulted in the vegetation model, where the richness of rare plant species increased with

increases in lodgepole pine and decreases in canopy cover index and large logs (adj. $R^2 = 0.251$) (Tables 141 and 142).

Regression Model for Common Plant Richness
   Individual regression models for the number of common plant species compared to each of the 3 environmental variable groups resulted in a 2-variable model for abiotic environment (positive association with precipitation and a negative association with west aspects; adj. $R^2 = 0.135$), no variables selected in relation to channel characteristics, and a 3-variable model for vegetation characteristics (positive associations with lodgepole pine and small logs, and a negative association with meadow; adj. $R^2 = 0.196$) (Table 140). These 5 key variables were entered into a backward stepwise regression, resulting in a 2-variable model, where the richness of common plant species increased with decreases in meadow and in association with west aspects (adj. $R^2 = 0.215$) (Tables 140 and 141).

TABLE 140. Variables selected in step-wise regressions between 3 groups of environmental variables ($n = 22$) and the number of plant species in each of 2 frequency classes. N = negative association and P = positive association at $P \leq 0.10$. Bolded = selected in the final regression at $P \leq 0.05$ on key variables from each group of environmental variables. Data were collected at sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996.

	Plant frequency class	
Environmental variable	Number of rare species	Number of common species
Abiotic environment:		
Precipitation	P	P
South aspects	N	-
West	-	**N**
Channel character:		
Gradient	N	-
Width	P	-
Vegetation character:		
Meadow	-	**N**
Lodgepole pine	**P**	P
Large log	**N**	-
Small log	-	P
Canopy cover index	**N**	**-**
Variables in final model	*3*	*2*
adj. R^2	*0.251*	*0.215*

TABLE 141. Final backwards regression model of key environmental variables related to plant species frequency class variables. Data were collected on sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996. Beta = partial regression coefficient.

Variable	B	SE of B	Beta	T	P
Number of rare plants:					
Canopy cover index	-0.076	0.024	-0.340	-3.168	0.002
Large log	-0.547	0.262	-0.205	-2.089	0.040
Lodgepole pine	4.150	2.065	0.215	2.010	0.048
Number of common plants:					
Meadow	-17.938	5.063	-0.354	-3.543	< 0.001
West aspect	-10.044	3.154	-0.318	-3.184	0.002

Plant Rarity by Environmental Gradients

The number of rare species was positively correlated with channel flow (physical factor 2), where as the number of common species was positively correlated with the other gradient, elevation–precipitation (Table 142). Both plant groups were positively associated with both gradients. The number of rare species was positively correlated with forest to meadow (vegetation factor 1) (Table 142). The number of common species was positively correlated with alder–willow (vegetation factor 3). Rare and common plant species had opposite relationships with the snag and log gradient (Table 142), with the number of rare species being negatively correlated, and the number of common species being positively correlated with the snags and logs.

TABLE 142. Significant ($P \leq 0.10$) correlations between plant frequency class variables and environmental gradients, as defined by principal components analysis. Bolded values indicate $P \leq 0.05$. N and P indicate non-significant (n.s.) negative and positive correlations, respectively. Data were collected on sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996.

	Number of rare species		Number of common species	
Environmental gradient	r	P	r	P
Physical gradient:				
1. Elevation–precipitation	0.146	0.197	**0.228**	**0.042**
2. Channel flow	**0.351**	**0.001**	0.050	0.663
Vegetation gradient:				
1. Forest to meadow	**0.388**	**<0.001**	-0.139	0.218
2. Subalpine vegetation	-0.037	0.746	0.012	0.915
3. Alder–willow	0.044	0.698	**0.319**	**0.004**
4. Aspen–cottonwood	-0.013	0.270	-0.125	0.270
Woody debris gradient:				
1. Snag and log	**-0.226**	**0.043**	**0.361**	**0.001**

Plant Rarity by Basin Orientation

I analyzed the variation in plant frequency class variables among basin orientations. The number of common species was different among basin orientations ($v = 3, 76$; SS = 4690.43, 14280.38; MS = 1563.48, 187.90; F = 8.32; $P < 0.001$). It was highest on the west side, followed

by the north, south, and was lowest in the east. The west and north sides had significantly more common species than the east side, and the west side also had significantly more common species than the south side. The number of rare species was similarly highest on the west side and lowest on the east side, but was not significantly different among orientations.

Patterns of Plant Beta Diversity

Plant Species Turnover along Environmental Gradients
Species Turnover

The lower of the gains and losses between any two segments represented beta diversity for the 2 segments - the change in composition that was independent from alpha diversity. The sum of beta diversity across all 3 segment comparisons, "total turnover", was used as the primary indication of the contribution of a gradient to beta diversity (Table 143). The elevation gradient had the highest total turnover ($n = 213$), followed by the snag and log ($n = 200$), channel flow ($n = 198$), alder−willow ($n = 195$), forest to meadow ($n = 193$), and subalpine vegetation ($n = 191$) gradients. The 2 remaining gradients had much lower total turnover.

TABLE 143. Beta diversity index values for plants within and among 9 environmental gradients. The number of species per segment, the number of species only occurring at upper ("gains") or lower ("losses") ends of the gradient, and Whittaker's (1972) beta diversity index (β_w) are displayed. A modified version of Whittaker's beta diversity index (β_{wMIN}) is also displayed. Bolded values indicate turnover. Data were collected on sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996.

Gradient	Richness of lower segment	Richness of higher segment	Total richness	Gains	Losses	$\beta_w{}^*$	β_{wMIN}†
Elevation:							
seg1:seg2	304	304	389	**85**	85	0.280	0.280
seg2:seg3	304	282	367	**63**	85	0.253	0.207
seg3:seg4	282	294	359	77	**65**	0.247	0.221
average						*0.260*	*0.236*
low:high	*389*	*359*	*470*	***81***	*111*	*0.259*	*0.211*
Precipitation:							
seg1:seg2	258	282	338	80	**56**	0.252	0.199
seg2:seg3	282	329	388	106	**59**	0.270	0.179
seg3:seg4	329	321	400	**71**	79	0.231	0.216
average						*0.251*	*0.198*
low:high	*338*	*400*	*470*	*132*	***70***	*0.276*	*0.178*
Elevation−precipitation:							
seg1:seg2	303	270	366	**63**	96	0.277	0.208
seg2:seg3	270	312	360	90	**48**	0.237	0.154
seg3:seg4	312	292	386	**74**	94	0.278	0.237
average						*0.264*	*0.200*
low:high	*366*	*386*	*470*	*104*	***84***	*0.253*	*0.220*

TABLE 143 cont.

Gradient	Richness of lower segment	Richness of higher segment	Total richness	Gains	Losses	$\beta_w{}^*$	β_{wMIN}†
Channel flow:							
seg1:seg2	277	281	339	62	**58**	0.215	0.206
seg2:seg3	281	306	368	87	**62**	0.254	0.203
seg3:seg4	306	335	413	107	**78**	0.289	0.233
average						*0.253*	*0.214*
low:high	*339*	*413*	*470*	*131*	*57*	*0.253*	*0.140*
Forest to meadow:							
seg1:seg2	256	283	342	86	**59**	0.269	0.208
seg2:seg3	283	312	376	93	**64**	0.264	0.205
seg3:seg4	312	339	409	97	**70**	0.257	0.206
average						*0.263*	*0.206*
low:high	*342*	*409*	*470*	*128*	*61*	*0.254*	*0.152*
Subalpine vegetation:							
seg1:seg2	332	287	385	**53**	98	0.244	0.160
seg2:seg3	287	283	352	**65**	69	0.235	0.226
seg3:seg4	283	305	378	95	**73**	0.286	0.239
average						*0.255*	*0.208*
low:high	*385*	*378*	*470*	*85*	*92*	*0.235*	*0.223*
Alder−willow:							
seg1:seg2	325	288	388	**63**	100	0.266	0.194
seg2:seg3	288	296	366	78	**70**	0.253	0.236
seg3:seg4	296	319	381	85	**62**	0.239	0.194
average						*0.253*	*0.208*
low:high	*388*	*381*	*470*	*82*	*89*	*0.225*	*0.214*
Aspen−cottonwood:							
seg1:seg2	308	312	387	79	**75**	0.246	0.236
seg2:seg3	312	256	367	**55**	111	0.290	0.173
seg3:seg4	256	313	362	106	**49**	0.272	0.157
average						*0.269*	*0.189*
low:high	*387*	*362*	*470*	*83*	*108*	*0.258*	*0.217*
Snag and log:							
seg1:seg2	324	286	394	**70**	108	0.292	0.216
seg2:seg3	286	303	368	82	**65**	0.250	0.215
seg3:seg4	303	284	368	**65**	84	0.254	0.215
average						*0.265*	*0.215*
low:high	*394*	*368*	*470*	*76*	*102*	*0.236*	*0.195*

* Whittaker's beta diversity index: $S/\alpha - 1$, where S = total species richness, and α = the average species richness of the two segments being compared.

† Modified Whittaker's beta diversity index: $(S/s\text{-}max) - 1$, where S = total species richness, and $s\text{-}max$ = the highest richness of the two segments being compared, resulting in a minimum beta diversity index value.

Patterns of turnover along each gradient provide additional insights as to their contributions to beta diversity based on presence (Table 143). Along the elevation gradient, total richness decreased from the lower to upper end of the gradient, and turnover was highest in at the lowest elevations. Both total richness and turnover increased along the precipitation gradient. The elevation−precipitation gradient had the lowest richness and turnover at mid gradient and the highest richness and turnover at the upper end of the gradient. As with the precipitation gradient, total richness and turnover increased along the channel flow, forest to meadow, and subalpine vegetation gradients. Along the alder−willow gradient, richness was lowest and turnover was highest at mid gradient. Turnover decreased along the aspen−cottonwood gradient, and richness was lowest at mid gradient. Total richness and turnover was highest at the lowest end of the snag and log gradient.

Whittaker's Index of Beta Diversity

The gradients were evaluated for their relative contribution to beta diversity in part based on a modified Whittaker's beta diversity index (β_{wMIN}), with the unmodified index value provided for comparison (Table 143). The average β_{wMIN} for segment comparisons along each gradient varied from a low of 0.189 for the aspen−cottonwood gradient to a high of 0.236 for elevation. Next to elevation, snag and log, and channel flow had the next highest values for the beta diversity index. The next 3 gradients were close in value: subalpine vegetation ($\bar{x} = 0.208$), alder−willow ($\bar{x} = 0.208$) and forest to meadow ($\bar{x} = 0.206$). The remaining gradients had average β_{wMIN} values of ≤ 0.200.

Species Presence

Species presence contributions to beta diversity were explored (Tables 144 to 146). Species contributing to gains and losses between lower and upper segments of each gradient are indicated, along with species showing additional trends of presence (absent from segment 1 or 4) along the gradient. Species specific associations with gradients also indicate the relevance of the gradient to individual species. The elevation gradient had a relatively equivalent number of species restricted to each end of the gradient, but only one species with frequency > 10% was restricted to one half of the elevation gradient: *Prunella vulgaris* (self-heal), a member of the mint family (Lamiaceae), appeared to be restricted to lower elevation reaches (Table 144). Seventeen additional species were absent from the most extreme reaches along the elevation gradient.

Over twice as many species were restricted to the upper end of the precipitation gradient compared to the lower end, including 5 species with frequency $\geq$ 10%: *Tsuga mertensiana* (mountain hemlock), *Spiraea densiflora* (mountain spirea), *Calochortus leichtlinii*, (Leichtlin's mariposa-lily) and *Erigeron coulteri* (fleabane) (Table 144). These species are restricted to more mesic environments within the basin. An additional 10 species with frequencies $\geq$ 10% were absent from the most xeric reaches. No species with frequencies $\geq$ 10% were absent from the upper half of the precipitation gradient, and only 3 species were absent from the most mesic reaches.

TABLE 144. Plant species present on ≥ 10% of all reaches and absent from lower or upper segments of each of 4 abiotic environmental gradients. Gradients were defined by principal components analysis. Data were collected on sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996.

Species	Elevation gradient low < --------------- > high				Precipitation gradient low < --------------- > high				Elevation–precipitation gradient low < ------------------ > high				Channel flow gradient low < ------------------ > high			
	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only
Actaea rubra		X			X				X							
Angelica californica			X												X	
Aster integrifolius			X								X					
Carex amplifolia										X						
Carex integra															X	
Calochortus leichtlinii								X								
Carex nervina			X													
Carex vesicaria															X	
Ceanothus prostratus		X								X						
Circaea alpina		X														
Cinna latifolia										X						
Sidalcea oregana		X														
Claytonia perfoliata																X
Dactylis glomerata															X	
Delphinium glaucum			X				X				X					
Dodecatheon alpinum							X				X					
Erigeron coulteri			X					X				X				
Galium trifidum		X								X						
Juncus balticus															X	
Juniperus occidentalis							X									
Lepidium virginicum										X						
Machaeranthera canescens															X	
Mertensia ciliata			X								X					
Mitella breweri							X									
Mimulus lewisii								X								
Mimulus moschatus							X				X					

TABLE 144 cont.

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Species	Elevation gradient low < ----- > high				Precipitation gradient low < ----- > high				Elevation–precipitation gradient low < ----- > high				Channel flow gradient low < ----- > high			
	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only
Paeonia brownii			X		X										X	
Phlox diffusa				—				—		X		—				
Phacelia hydrophylloides							X									
Populus balsamifera										X						
Prunella vulgaris	X									X						
Pyrola asarifolia										X						
Ranunculus alismifolius															X	
Ranunculus occidentalis										X						
Salix lucida		X								X						
Sambucus melanocarpa			X				X				X					
Scirpus microcarpus										X						
Sidalcea glaucescens							X								X	
Sidalcea oregana										X						
Smilacina racemosa							X									
Sorbus californica							X									
Spiraea densiflora								X								
Tragopogon dubius						X										
Trifolium monanthum			X													
Tsuga mertensiana			X					X				X				
Valeriana californica										X						
Total, frequency ≥ 10%	1	6	11	0	0	3	10	5	0	13	9	2	0	0	9	1
Total, frequency > 1	34	19	26	28	19	23	15	52	19	29	22	39	16	18	14	42

Much like the precipitation gradient, approximately twice as many species were absent from the lower end of the gradient compared to the upper end of the elevation−precipitation gradient (Table 144). Two species with frequencies $\geq$ 10% were absent from the lower half of the elevation−precipitation which were also absent from the lower half of the precipitation gradient: *Erigeron coulteri* and *Tsuga mertensiana*. Nine additional species were absent from the lowest segment of the elevation−precipitation gradient, all but 2 of which were similarly associated with the elevation or precipitation gradients. Alternatively, 13 species were absent from the highest reaches on the elevation−precipitation gradient.

Over twice as many species were absent from the lower half of the channel flow gradient (Table 144), but only one occurred on $\geq$ 10% of all reaches: *Claytonia perfoliata* (miner's lettuce) was absent from the lower half of the channel flow gradient, indicating that it is restricted to low gradient, wide streams that have greater accesss to floodplains. Nine additional species were absent from the lowest channel flow reaches.

Although many species were absent from upper or lower segments of the snag and log gradient, no species with frequencies $\geq$ 10% were absent from the upper or lower halves of either gradient (Table 145). Along the snag and log gradient, 6 species the frequencies $\geq$ 10% were absent from one of the most extreme snag and log segments.

TABLE 145. Plant species present on $\geq$ 10% of all reaches and absent from lower or upper segments of the snag and log gradient (derived by principal components analysis). Data were collected on sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996.

	Snag and log gradient			
	low < ---------------------- >			
		high		
	Seg.	Seg.	Seg.	Seg.
	1&2	1,2,3	2,3,4	3&4
Species	only	only	only	only
Claytonia perfoliata		X		
Salix lucida		X		
Prunus virginiana			X	
Mimulus moschatus			X	
Penstemon gracilentus			X	
Actaea rubra			X	
Total, frequency $\geq$ 10%	0	2	4	0
Total, frequency > 1	25	12	17	21

A total of 30 species with frequencies $\geq$ 10% were restricted to one end of one or more vegetation gradients (Table 146). Along the forest to meadow gradient, 3 times as many species were absent from the forest end of the gradient compared to the meadow end. However, no species with frequencies $\geq$ 10% were absent from the upper or lower half of the gradient. A total of 15 species were absent from either the lowest or highest segment reaches. The 6 species absent from highest reaches represent those species unassociated with meadow environments, where as the 9 species absent from the lowest reaches represent forest specialists. A relatively equivalent number of species were absent from each end of the subalpine vegetation gradient. One species with a frequency $\geq$ 10% was absent from the upper half of the gradient, *Cinna latifolia* (drooping woodreed). An additional 7 species with frequencies $\geq$ 10% were absent from

the most extreme segments at either end of the subalpine vegetation gradient. Similar to the subalpine vegetation gradient, an equivalent number of species were absent from each end of the alder−willow vegetation gradient. However none of these species were present on ≥ 10% of the reaches. Five species with frequencies ≥ 10% were absent from one of the segments at the most extreme ends of the alder−willow gradient. Approximately twice as many species were restricted to the lower half of the aspen−cottonwood gradient compared to the upper half of the gradient, and 2 of these species were present ≥ 10% of the reaches: *Sorbus californica* (California mountain ash) and *Holodiscus discolor* (oceanspray). An additional 8 species with frequencies were ≥ 10% were absent from either the highest or lowest end of the gradient.

TABLE 146. Species present on $\geq$ 10% of all reaches and absent from lower or upper segments of each of 4 vegetation gradients. Gradients were defined by principal components analysis. Data were collected on sample reaches (n = 80) in the Lake Tahoe basin, 1995 to 1996.

Species	Forest to meadow gradient low < ----------------- > high				Subalpine vegetation gradient low < ----------------- > high				Alder–willow gradient low < ---------------- > high				Aspen–cottonwood gradient low < ---------------- > high			
	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only
Actaea rubra		X			X										X	
Arabis rectissima														X		
Carex heteroneura			X													
Carex integra			X													
Cinna latifolia					X									X		
Circaea alpina		X														
Dodecatheon alpinum			X													
Dryopteris arguta		X					X			X						
Eriogonum umbellatum			X													
Erysimum capitatum											X					
Galium trifidum															X	
Holodiscus discolor		X											X			
Ipomopsis aggregata		X								X						
Lepidium virginicum						X										
Mertensia ciliata											X					
Mimulus lewisii			X													
Mimulus moschatus			X													
Paeonia brownii							X								X	
Penstemon gracilentus														X		
Phlox gracilis		X														
Polygonum bistortoides			X													
Prunella vulgaris											X					
Pyrola asarifolia						X										
Ranunculus alismifolius						X										
Ribes lasianthum			X													
Sidalcea oregana						X										
Sorbus californica													X			
Spiraea densiflora														X		

TABLE 146 cont.

Species	Forest to meadow gradient low < ----------------- > high				Subalpine vegetation gradient low < ----------------- > high				Alder−willow gradient low < ---------------- > high				Aspen−cottonwood gradient low < ---------------- > high			
	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only
Trifolium monanthum			X													
Tsuga mertensiana															X	
Total, frequency $\geq$ 10%	0	6	9	0	1	5	2	0	0	2	3	0	2	5	3	0
Total, frequency > 1	14	21	19	45	26	20	10	21	20	9	15	21	41	16	12	20

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Ranking Gradients for Beta Diversity

The 8 environmental gradients were ranked to reflect their contribution to beta diversity based on species presence data (Table 147). The elevation gradient had the highest total turnover, which also had the second highest core turnover and average β_{wMIN}. The snag and log gradient ranked next highest in beta diversity, but had relatively low core turnover. The next 4 gradients were close in total turnover, but varied in their core turnover from high to low in the following order: forest to meadow, channel flow, subalpine vegetation, and alder−willow. The remaining 2 gradients had much lower values for total turnover.

TABLE 147. Ranking of environmental gradients by their contribution to plant beta diversity based on presence. Data were collected on sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996.

Environmental gradient	Total turnover	Core turnover - freq. ≥ 2 reaches	Average β_{wMIN}	Rank
Elevation	213	107	0.236	1
Snag and log	200	75	0.215	2
Channel flow	198	90	0.214	3
Alder−willow	195	65	0.208	4
Forest to meadow	193	99	0.206	5
Subalpine vegetation	191	77	0.208	6
Precipitation	186	109	0.198	7
Aspen−cottonwood	179	89	0.189	8

Plant Species Turnover by Basin Orientation

Basin orientation can affect species turnover, as did the environmental gradients analyzed above. All pair-wise comparisons of orientations were conducted to assess the contribution of basin orientation to species turnover (Table 148). Based on the average β_{wMIN} across all orientation comparisons, orientation had a moderate contribution to beta diversity compared to the environmental gradients analyzed. The greatest species turnover occurred between the north and east orientations, with a total turnover of 70 and a high index value of 0.260. It was not possible to compare patterns of species turnover between basin orientation and the other gradients because orientations can not be aligned along a linear gradient, however the comparison of east−dry and west−wet orientations provides a representation of all orientation comparisons, and the species turnover between these sides of the basin was relatively high ($n = 80$).

TABLE 148. Beta diversity index values for plants among basin orientations. The number of species per segment, the number of species only occurring at upper ("gains") or lower ("losses") ends of the gradient, and Whittaker's beta diversity index (β_w) are displayed. A modified version of Whittaker's beta diversity index (β_{wMIN}) is also displayed. N = north, E = east, S = south, W = west side of the basin. Data were collected on sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996.

Basin orientation	Richness of first segment	Richness of second segment	Total richness	Gains	Losses	β_w*	β_{wMIN}†
N:E	269	264	339	**70**	75	0.272	0.260
E:S	264	294	363	99	**69**	0.301	0.235
S:W	294	322	391	97	**69**	0.269	0.214
N:S	269	294	366	97	**72**	0.300	0.245
E:W	264	322	384	120	**62**	0.311	0.193
N:W	269	322	370	101	**48**	0.252	0.149
average						*0.284*	*0.216*
N and E:S and W	*339*	*391*	*471*	*132*	**80**	*0.290*	*0.205*

* Whittaker's beta diversity index: S/α - 1, where S = total species richness, and α = the average species richness of the two segments being compared.

† Modified Whittaker's beta diversity index: (S/s-max) - 1, where S = total species richness, and s-max = the highest richness of the two segments being compared, resulting in a minimum beta diversity index value.

Species absent from one or more orientations provide species specific contributions to the gains and losses observed between orientations. A total of 339 species occurred on more than one reach, and 175 of these were absent from one or more orientations. The east side of the basin had the greatest number of species missing ($n = 101$), followed by the north side ($n = 90$), south side ($n = 88$), and finally the west side ($n = 48$). The west side had substantially fewer species absent compared to the other orientations.

Species with frequencies ≥ 10% were examined in more detail to explore potential ecological phenomena responsible for observed disjunct distributions (Table 149). A total of 26 plant species had frequencies ≥ 10% and were absent from one or more orientations. The highest number of species with > 10% frequency were absent from the east side of the basin, and most of these (11 of 15) were only absent from the east side. These species, as well as the one additional species absent from both the north and east sides of the basin (*Spiraea densiflora,* Mountain spirea), are likely to be restricted by moisture availability. Conversely, 2 species were absent from only the west, *Chrysothamnus nauseosus* (rabbitbrush) and *Lathyrus lanszwertii* (Nevada pea), with one additional species, *Paeonia brownii* (wild paeonia), absent from both the south and west. These species are likely to be restricted to more xeric or warm conditions. Three species were absent from east and south sides of the basin: *Phacelia hydrophylloides* (baldhead phacielia), *Mimulus moschatus* (musk monkeyflower), and *Prunella vulgaris* (self-heal).

TABLE 149. Plant species occurring on $\geq$10% of all reaches and absent from one or more basin orientations. X's indicate where species was present. Sample reaches per orientation are indicated. Data were collected on sample reaches (*n* = 80) in the Lake Tahoe basin, 1995 to 1996.

| Species | Presence by basin orientation | | | |
| | Xeric < -- > Mesic | | | |
	North side (*n* = 20)	East side (*n* = 20)	South side (*n* = 16)	West side (*n* = 24)
Calochortus leichtlinii	X		X	X
Calyptridium monospermum	X	X		X
Chrysothamnus nauseosus	X	X	X	
Cinna latifolia		X	X	X
Corallorhiza maculata		X	X	X
Delphinium glaucum	X		X	X
Dodecatheon alpinum	X	X		X
Eriogonum umbellatum	X		X	X
Juniperus occidentalis	X		X	X
Lathyrus lanszwertii	X	X	X	
Lonicera conjugialis	X		X	X
Lonicera involucrata	X		X	X
Mimulus moschatus	X			X
Orthilia secunda		X	X	X
Paeonia brownii	X	X		
Phlox gracilis	X	X		X
Phacelia hydrophylloides	X			X
Polygonum bistortoides	X	X		X
Polemonium californicum	X		X	X
Polygonum phytolaccifolium	X	X		X
Prunella vulgaris	X			X
Sambucus racemosa	X		X	X
Sidalcea glaucescens	X		X	X
Sorbus californica	X		X	X
Spiraea densiflora			X	X
Tsuga mertensiana	X		X	X
Sum of absent species	*4*	*15*	*9*	*3*

Concordance Among Diversity Measures

Measures of Alpha Diversity

All correlations between diversity measures were positive and significant (Table 150). The strongest correlations were between common species richness, upland species richness, and total species richness, indicating that patterns of species richness were driven by common, upland species. Rare and common species richness were equivalently correlated with aquatic−riparian−meadow species richness, but common species richness was more strongly correlated with upland than riparian richness. This indicates that aquatic−riparian−meadow species constitute a combination of rare and common species, but that most rare species are also aquatic−riparian−meadow associates.

TABLE 150. Correlations between 5 variables describing plant diversity in the Lake Tahoe basin. Bolded values indicate $P \geq 0.05$. Dashes indicate irrelevant significance values. Shaded areas indicate redundant areas of the correlation matrix. Data were collected on sample reaches ($n = 80$) in the Lake Tahoe basin, 1995 to 1996.

Plant diversity variables	Plant species richness		Aquatic–riparian–meadow species richness		Upland species richness		Rare species richness	
	r	P	r	P	r	P	r	P
Plant species richness								
Aq–rip–mdw richness	0.819	<0.001						
Upland richness	0.805	<0.001	0.318	0.004				
Rare species richness	0.606	<0.001	0.664	<0.001	0.314	0.005		
Common species richness	0.953	<0.001	0.717	<0.001	0.833	<0.001	0.337	0.002

Alpha and Beta Diversity

An average of 285.2 (range = 256 to 321, SE = 3.53) plant species were shared among segments ($n = 20$ reaches per segment), based on segment comparisons across all 8 environmental gradients. The average richness lost or gained between segments was 24.3 species (range = 0 to 57, SE = 3.30), and it was significantly lower (based on paired t-test across gradients, t = 8.93, $P < 0.001$) than the average number of species turnovers between segments ($\bar{x}$ = 64.8 species, range = 49 to 85, SE = 1.69). The average number of species shared among segments constituted 60.7% of all species observed, and average richness and species turnover constituted 5.2% and 13.8%, respectively, of all species observed.

The analysis of the relative influence of environmental gradients on gamma diversity in the basin showed that the forest to meadow gradient had the greatest contribution to gamma diversity in the basin (Fig. 59). The forest to meadow gradient showed a shift in 276 species along its length, comprising close to 60% of the total plant flora. The diversity associated with the forest to meadow gradient was primarily driven by species turnover, responsible for approximately 2/3 of the shifts in species along the gradient. The positive relationship observed between richness and the forest to meadow gradient was not reflected in the alpha diversity analysis. Upon further inspection, positive relationships were observed between alpha diversity and lodgepole pine, but a negative relationship was observed with meadow. Investigation of the frequency of occurrence per species per segment revealed that frequency of occurrence declined while species richness increased from segment 1 to 4 (r = -0.895, $P = 0.105$), thus frequency of occurrence per reach masked increases in species richness along the forest to meadow gradient.
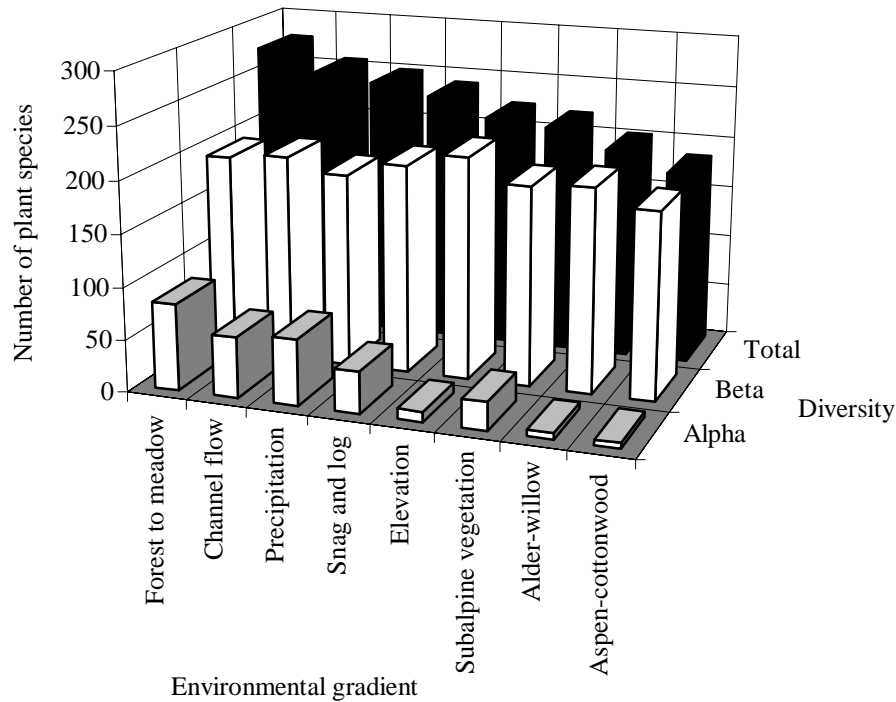
FIG. 59. Contribution of each of 9 environmental gradients to plant species diversity in the Lake Tahoe basin. Total change in composition is shown, along with the composite contributions of alpha and beta diversity. Data were collected on 80 sample reaches in 1995 to 1996.

The forest to meadow gradient was followed in its contribution to gamma diversity by 3 gradients with similar contributions to diversity: channel flow, channel logs, and precipitation (FIG. 59). The relationship between plant diversity and channel logs is assumed to simply represent changes in channel flow since all plants were riparian or terrestrial (as opposed to aquatic) and channel flow and channel logs were so similar in their diversity. Channel flow had a similar level of beta diversity as the forest to meadow gradient, but a slightly lower contribution from alpha diversity. Like the forest to meadow gradient, the positive relationship between richness and channel flow did not surface in the analysis of alpha diversity based on richness per reach. Investigation of the frequency of occurrence per species per segment revealed that frequency of occurrence declined while species richness increased from segment 1 to 4 (r = -0.979, P = 0.021), thus frequency of occurrence per reach masked increases in species richness along the channel flow gradient.

Precipitation had the fourth highest contribution to gamma diversity. It had one of the greatest balances between beta and alpha diversity, next to the forest to meadow gradient, and positive relationships between richness and precipitation were consistent with relationships observed between precipitation and alpha diversity in earlier analyses.

The remaining gradients had much lower contributions to gamma diversity (FIG. 59). The snag and log gradient showed 240 species shifting along its length, being mostly contributed by beta diversity. Elevation, subalpine vegetation, and alder−willow had at least 50 fewer species shifting along their lengths than the forest to meadow gradient, with beta diversity making the greatest contribution to changes in species composition. Finally, aspen−cottonwood ranked last in contributions to gamma diversity, far below the next highest gradient with only 184 species

shifting along this gradient and all of them attributed to turnovers. Aspen−cottonwood as a variable, rather than a gradient, was positively associated alpha diversity in earlier analyses. Apparently a positive relationship did exist between plant richness and aspen−cottonwood but this relationship becomes muddled when aspen−cottonwood is analyzed as a gradient. The difference in compositional change among the gradients ranged as high as 92 species-- approximately 20% of the observed total species richness.

The total change in composition was significantly correlated with alpha diversity (r = 0.943, $P = < 0.001$), but was not correlated with beta diversity (r = 0.247, $P = 0.555$), and alpha and beta diversity were not correlated with each other (r = -0.089, $P = 0.834$). In general, net changes in richness (alpha diversity) along gradients were lower but more variable ($\bar{x} = 36.5$, SE = 10.40) than changes in composition (beta diversity) ($\bar{x} = 194.4$, SE = 3.57).

DISCUSSION

Environmental Influences on Plant Diversity

I encountered a high number of plant species ($n = 470$), comprising approximately 44% of all plant species known to occur in the Lake Tahoe basin, despite the fact that I sampled only within stream-side environments. Only 45% of all plant species detected were considered aquatic, riparian, meadow associates, indicating that riparian-associated vegetation was often less than 30 m in width, and upland-associated plant species commonly occurred within 30 m of stream channels. The number of plant species shared among reaches was low, with an average of only 15.1% (ranging from 7.0% to 28.3%) of all species occurring on any given reach. Similarly, turnover averaged 16.3% from lower to upper half of the 8 environmental gradients examined. Therefore, richness and turnover both contributed substantially to the diversity of plant species. Several environmental features were associated with each measure of plant species diversity in the Lake Tahoe basin.

The diversity of plant species was greatest in association with meadow, lodgepole pine, the forest to meadow gradient, and the channel flow gradient. Forest to meadow gradient was demonstrated in Chapter 4 to be significantly positively correlated with the channel flow, indicating that the greatest diversity of plants occurred among the diversity of vegetation types and channel flow characteristics at low to mid elevation sites. Precipitation, and elevation were strongly associated with one, but not both elements of diversity (richness and turnover, respectively). These relationships are discussed in more detail below.

The forest to meadow gradient ranked the highest in its contribution to diversity in the Lake Tahoe basin. Interestingly, the forest to meadow gradient was not associated with particularly high richness or turnover. Rather, it was a major contributor to diversity through the combined contributions of richness and turnover. It is not surprising that the strongest vegetation gradient would be associated with the highest diversity. Although increases in richness were observed from low to high segments of the forest to meadow gradient, I did not observe a correlation between plant species richness and the forest to meadow gradient. Upon closer examination, it was apparent that the average frequency of occurrence of plant species decreased from forests to meadows. Thus, although the number of species per reach was not greater in meadows compared to mixed conifer, plant species composition varied more among meadows and lodgepole pine forests than among mixed conifer forests, resulting in meadows contributing more to the diversity of plant species than mixed conifer forests. Most meadows adjacent to streams are moist, and in these conditions, sedges and rushes are likely to dominate most other species resulting in lower species richness per meadow. However, the high diversity of sedges and rushes in the Sierra Nevada and the Lake Tahoe basin could readily result in high plant species

diversity among meadows. The frequent co-occurrence of meadow with lodgepole pine (meadow was present on 76% of all reaches with lodgepole) makes the combination of these two vegetation types a strong contributor to plant species diversity in the basin.

Two additional vegetation types were positively associated with one or more measures of alpha diversity: aspen−cottonwood and alder−willow. Aspen−cottonwood was positively associated with plant species richness and aquatic−riparian−meadow richness in particular. Aspen−cottonwood is known for its high species richness (DeByle and Zasada 1980) which is attributed to its affiliation with moist environments. It provides a uniquely rich environment at the intermediate elevations where it occurs in the Lake Tahoe basin. Alder−willow was also positively associated with the richness of aquatic−riparian−meadow species. Alder−willow vegetation is the predominant woody component of the montane riparian vegetation in the Lake Tahoe basin, and it occurred frequently (over 95% of all sample reaches) but typically occupied a small proportion of the reach (average < 20%). Alder−willow is typically a compositionally simple vegetation type, and the positive association with aquatic−riparian−meadow richness suggests that a unique set of plant species are associated with alder−willow environments, as well as the environmental conditions that support alder−willow.

Channel flow had a substantial influence on plant species diversity, and its influence is strongly related to the diversity patterns observed in association with the forest to meadow gradient. Channel flow did not surface as strongly associated with shifts in richness, however species turnover was greater at higher channel flows and species richness per segment increased steadily from low to high channel flow. As observed with the forest to meadow gradient, species richness per reach did not vary significantly because species had a lower frequency of occurrence on reaches with high channel flow characteristics. Thus, low gradient, wide channels were associated with a rich and heterogeneous environment that provided for relatively high diversity of plant species, particularly aquatic, riparian, and meadow associates.

When richness and turnover were considered individually, precipitation and elevation surfaced as the strongest influences on plant diversity. Plant species richness increased substantially in response to increased moisture as represented by precipitation and aspect. Precipitation was the only variable that had the same relationship with both rare and common species, suggesting that it affects all plant species in a similar manner, but the lack of relationship with upland species suggests that it affects upland species to a lesser degree than species more closely associated with mesic environments. Turnover was highest in association with the elevation gradient, along which temperature, length of growing season, and atmospheric moisture are known to vary (Whitney 1979). In addition, it was apparent that turnover was higher between and within lower elevation segments compared to higher elevation gradients. The number of core turnovers along the elevation gradient was second only to precipitation, indicating that elevation had a fundamental influence on the composition of plant species. High elevation species absent from the lowest elevation reaches, such as *Tsuga mertensia* (mountain hemlock), *Pinus albicaulis* (white bark pine), and *Paeonia brownii* (wild paeonia), are contributing to the high turnover observed between lower elevation segments, and low elevation species absent from the highest elevation reaches, such as *Prunella virginiana* (western choke cherry) and *Galium trifidum* (sweet-scented bedstraw), are contributing to the turnover observed between higher elevation segments.

It is likely that turnover along the elevation and precipitation gradients reflected the limits of environmental tolerance of species. Examination of the relationship between precipitation and richness showed a marked curvilinear relationship, expressed in total plant species richness, as well as aquatic−riparian−meadow species richness, and common species richness. Such a curvilinear relationship could be interpreted as reflecting the "paradox of enrichment" response (Huston 1979, Rosenzweig and Abramsky 1993). However in the Lake Tahoe basin, high

precipitation coincides with high elevation, negating some of the potential gain in productivity that may have accompanied increased precipitation. Higher richness associated with the mesic, west side of the basin versus lower richness associated with the xeric, east side of the basin provides further evidence that moisture is the primary limiting factor for most plant species. The west and north sides also had the greatest number of unique species (high beta diversity), most of which were rare (i.e., low frequency of occurrence).

Snags and logs, like elevation, were not associated with richness, but were associated with high turnover. Richness had a bimodal relationship with snags and logs, being high in the lowest segment of the gradient (segment 1), coinciding with the occurrence of meadow environments, and high again in the second highest segment (segment 3), where snag and log densities in forested environments appeared to reach some optimum value for many plant species. Further, higher turnover at the lower end of the snag and log gradient suggests that greater heterogeneity of environments existed where woody debris, particularly logs, were less abundant.

Variation Among Species Groups

Species groups were valuable in discerning finer patterns of association in alpha diversity in this study, as they have in other studies (e.g., Minchin 1989). The equivalent strength of the correlation of aquatic−riparian−meadow and upland species richness with total species richness indicates that even within the narrow width of the sample reaches (30 m on either side of the channel) upland-associated plant species were as prevalent (number and frequency) as aquatic−riparian−meadow-associated plant species.

Environmental relationships of each habitat group were, of course, closely aligned with their associated habitats. Aquatic−riparian−meadow and upland associates had opposing relationships with channel gradient and mixed conifer. Aquatic−riparian−meadow richness was greater in association with wide, low gradient streams, whereas common species decreased in richness in association with these same channel flow characteristics. The 2 groups also had opposing relationships with forest to meadow gradient and mixed conifer (which represented the forest end of the forest to meadow gradient), with aquatic−riparian−meadow species richness being greater in association with the meadow end of the gradient. The richness of aquatic−riparian−meadow species was not only greater in areas with higher precipitation, but also sensitive to aspect, having greater richness on less exposed, presumably more mesic east aspects. Thus, aquatic−riparian−meadow species were more sensitive to the availability of moisture than upland species.

Although most environmental relationships of the two plant groups were as expected, a few were informative. It was somewhat surprising that aquatic−riparian−meadow species richness had stronger relationships with lodgepole pine than meadow, the 2 vegetation types associated with the "meadow" end of the forest to meadow gradient. Fendler's meadow-rue is commonly associated with lodgepole pine, and it was the second most frequent species detected in the study area. It is likely that other members of the lodgepole pine understory are common aquatic−riparian−meadow species, and that lodgepole pine had a higher average richness of species than meadows. Meadows encountered in the study area were primarily wet meadows, which are often dominated by a few species.

Even though over 60% of all species were rare, common species had a strong influence on the environmental relationships exhibited by total species richness. The low correlations between rare and common species richness, and between aquatic−riparian−meadow and upland species richness provide the opportunity to identify environmental influences that operate across all species when they affect both groups associated with either of these 2 characteristics. I found that only precipitation and lodgepole pine were similarly positively associated with rare and

common species richness, demonstrating that these 2 environmental features influence a broad array of plant species. Based on high correlations between rare and aquatic−riparian−meadow, as well as between common and upland species, it is clear that aquatic−riparian−meadow species were relatively rare compared to upland species. Indeed, 3 of the 6 most common species were dominant woody species, including white alder, white fir, and Jeffrey pine.

Rare and common species had very different environmental associations. Both rare and common species richness increased with increases in precipitation, but they had unique relationships with many other environmental features, particularly vegetation. Generally, rare species richness was positively associated with lodgepole pine and meadow and higher channel flows, whereas common species richness was positively associated with woody vegetation (conifer forests and alder−willow) and lower channel flows. These patterns of association are consistent with those observed for aquatic−riparian−meadow and upland species richness, respectively.

Conservation and Management Implications

The richness of plant species in the riparian areas I studied (n = 470 species) and the number of plant species per sample reach (range = 33 to 133 plants/reach) were comparable to, or greater than, many similar studies of richness and biological diversity in riparian ecosystems at lower elevations. Zimmerman at al. (1999) looked at vegetation diversity along a riparian system in Arizona, and found only 92 species of plants in the canyon system they studied. Similarly, Nilsson et al. (1988) found a range of just 41 to 115 species of plants along the 4 rivers studied in Sweden, and Pollock et al. (1998) found only 233 species of plants occurring within with riparian systems they studied in southeast Alaska. However other studies report an equivalent or greater number plant species, such as Planty-Tabacchi et al. (1996) who found vascular plant species richness to range from 254 to 684 species along 3 river corridors in Oregon and Washington, all of which were generally located at lower elevations that those characterizing the Lake Tahoe basin. The high richness of plant species encountered in the stream-side riparian areas of the basin is probably a reflection of the high richness of plant species in the Sierra Nevada (Stebbins and Major 1965, Raven and Axelrod 1978). Plants comprise an important food and substrate base for higher trophic levels and managing to conserve their diversity may also serve to maintain their functional role in riparian environments.

Vegetation characteristics had a substantial influence on plant species diversity, and, based on the relative number of significant relationships, exerted an influence on plant species diversity equivalent to that of the physical environment. Given that richness and turnover both contributed greatly to the diversity of plant species in the Lake Tahoe basin, and the primary influence that vegetation had on plant species diversity, conservation of plant diversity would require areas large enough to support the richness of a site, and the establishment of many area such that the full diversity of vegetation types were represented. A greater number of areas at lower elevations, focusing on meadow, lodgepole pine, and aspen−cottonwood in particular, is called for based on the greater among-reach diversity exhibited by these vegetation types and lower elevation reaches in general.

Lodgepole pine is one of the most life-form diverse vegetation types, consisting of a forested overstory, a grass and herb understory, and frequently peppered with patches of shrubs (Potter 1994). The high richness and turnover associated with lodgepole and the forest to meadow gradients is consistent with these characterizations. Other upper montane and subalpine vegetation types generally lack a prevalence of one or more of these components (Bartolome 1988, Potter 1994). The fact that reaches with > 10% lodgepole pine consistently supported at least 50 plant species (17 species higher than the lowest richness) shows that lodgepole pine has a strong influence on plant species richness.

Any effort to conserve the richness and diversity of plant species in the Lake Tahoe basin would benefit from special management considerations for lodgepole pine, particularly in

proximity to streams and meadows. The higher richness of aquatic, riparian, and meadow-associated plant species in association with lodgpole pine indicates that the occurrence of riparian woodland vegetation may not be a good indicator of environments important in the support of aquatic, riparian, or meadow species. In the Lake Tahoe basin, it may be more prudent to consider the potential impacts of management on riparian species based not on "indicator" vegetation types, but rather based on a given distance from the stream, potentially modified by slope and aspect. In terms of lodgepole pine management, potential impacts include cattle grazing and fire management. Lodgepole pine is the most common invader in montane meadows (Whitney 1979) and the lack of fire in the basin may be resulting in a greater prevalence of lodgepole pine forests. Fire is likely to play an important role in maintaining the vigor and diversity of lodgepole pine and meadows, as well as a mutual balance in their extents.

Meadows are typically considered highly productive environments, particularly at lower elevations (Crane 1950), but in this study they did not individually support a high diversity of plant species. It is probable that historically heavy grazing by sheep and cattle throughout the Sierra Nevada (McKelvey and Johnston 1992), including the Lake Tahoe basin (Lindström 2000), combined with continued lower levels of grazing in most wet meadows throughout the basin, have impacted the diversity of plant species currently occurring in wet meadow habitats. Grazing can decrease the diversity and density of native plant species (e.g., Fleischner 1994). The greatest threats to meadow condition and extent are lack of fire, which can affect succession, and water diversions and grazing, which can affect the hydrodynamics of meadows (Ratliff 1985). Agencies within the Lake Tahoe basin are increasing the use of prescribed fire in an attempt to restore the function of fire in reducing flammable fuels. Prescribed fires and wildfires that are allowed to burn should generally improve the quality and quantity of meadows in the basin. Water diversions are rare in the basin, but channel restoration efforts are relatively common (TRPA 1997), and future efforts should consider potential impacts on meadow systems. Most meadows in the basin are currently grazed by cattle, and few allotments exclude cattle from grazing adjacent to stream channels (USDA 1988). Grazing can have a deleterious effect on many plant species.

Aspen-cottonwood had a positive influence on plant species richness equivalent to that of lodgepole pine. As seen with lodgepole pine, a minimum of 60 plant species (27 species greater than the lowest richness) occurred when aspen–cottonwood exceeded 10%, and a minimum of 20 aquatic–riparian–meadow species (15 species grater than the lowest richness) occurred whenever aspen–cottonwood was present. Aspen communities are considered highly productive environments and are known for their high plant species richness (DeByle and Winokur 1985). Given the high diversity of plant species and relative rarity of aspen–cottonwood in the Lake Tahoe basin, management of these stands could substantially affect plant species diversity. Maintaining natural processes, such as nutrient cycling, succession, and fire, and minimizing human-related disturbances, such as grazing and mountain biking, are the most likely means by which plant species richness might be conserved in aspen–cottonwood stands. Aspen stands are sometimes ephemeral vegetation associations which are succeeded by conifer forests in the absence of fire. However, depending on soils and moisture, some aspen stands can be relatively permanent features even in the absence of fire (Barry 1971, Youngblood and Mueggler 1981, Mueggler and Campbell 1982). In the Lake Tahoe basin, it is possible that the lack of fire has reduced the extent of aspen, and that grazing has reduced the richness of plant species. The increased use of prescribed fire and proportion of wildfires that are allowed to burn, and limited or no grazing are measures that are likely to improve the biological integrity and perhaps the extent of aspen stands in the basin.

Alder–willow contributed to the richness of aquatic–riparian–meadow plant species. Alder and willow are often noted as having high species richness (e.g., Sawyer and Keeler-Wolf 1995), and it is to be expected that riparian-associated species would be more speciose in riparian-associated vegetation. Alder and willow occurred frequently along stream reaches, and was generally well distributed throughout the Lake Tahoe basin. Management activities are unlikely to change the distribution of alder and willow, however grazing and channel restoration could alter its vigor and abundance (Fleischner 1994). Restoration efforts that involve key meadow

complexes with well developed alder and willow vegetation should be carefully considered so as to avoid detrimental effects on riparian and meadow bird habitat.

A high density of small snags and logs occurs in the Lake Tahoe basin as a result of recent large-scale tree mortality events (Weatherspoon et al. 1992, McKelvey et al. 1996, Manley et al. 2000), as evidenced by the high frequency of occurrence (> 80%) of large snags and both sizes of logs across all sample reaches. Existing stands of dense, small-diameter snags and logs appeared to have low suitability for some plant species. And as with elevation, turnover was higher between and within lower segments of the snag and log gradient compared to higher segments along the gradient. High turnover along the snag and log gradient suggests that species are variously adapted to woody debris and the occlusion of bare mineral soil, as well as the types of environments with greater or lesser amounts of woody debris. High densities of woody debris, particularly logs, are likely to occlude ambient light from reaching mineral soil, reducing the ability for plants to become established or to maintain themselves. Management of woody debris to benefit plant diversity should focus on reducing uncharacteristically highest densities resulting from lack of fire, and but otherwise maintaining a range of densities. Fire management to reduce the risk of fire in the Lake Tahoe basin is likely to create more favorable conditions for plant species diversity in the basin.

Riparian associates (i.e., aquatic–riparian–meadow species) and rare species were more speciose in association with greater channel flow. Zimmerman et al. (1999) found that understory plant diversity decreased with increasing slope of stream banks (correlated with channel gradient in my study area). They attributed this relationship to increased sun and warmth in low slope sites and increased microhabitat heterogeneity. Microhabitat heterogeneity was shown to create a patchy distribution of obligate and facultative riparian species in New Mexico (Dick-Peddie 1993). Distribution, abundance, and diversity of smaller perennial plants are commonly more sensitive to geomorphic heterogeneity than overstory species (Burnette et al. 1998, Nichols et al. 1998). Because of the sensitivity of plant species to soil moisture and inundation, the typically high variety of microhabitats within a single floodplain can support a broad array of plant species and assemblages. It then follows that low gradient, wide streams with larger floodplains would support high plant species richness (e.g., Planty-Tabacchi et al. 1996). It is likely that the increased plant species richness I observed in association with wide, low gradient reaches reflects aquatic and riparian habitat heterogeneity. Competition for the use of floodplains, particularly at the mouths of streams near Lake Tahoe, is high because they are flat and have rich soils. For example, the city of South Lake Tahoe occupies much of the floodplain of the largest stream flowing into Lake Tahoe, the Upper Truckee River. Losses from development are compounded by uses such as grazing and recreation, which can readily impact plant species diversity (Ratliff 1985, Fleischner 1994). Floodplain management should be a key focal point in the conservation of plant species diversity in the Lake Tahoe basin.

Plants species richness is commonly greater in association with more mesic conditions. For example, Lapin and Barnes (1995) found that most moist and nutrient rich ecosystems had the highest richness of plant species, and Rey Benayas et al. (1999) similarly found that species richness of plants was positively correlated with soil wetness and wetness variation. Given that plants were more speciose, and a greater proportion of plants were rare on the mesic, west side of the basin, management activities on the west side of basin should apply greater concern and consideration to plant species diversity, particularly in regard to fire management, which can dramatically change soil moisture characteristics.

Based on the curvilinear relationship observed between plant species richness and precipitation, moisture may be the most limiting factor at lower elevations; however, at the highest elevations, temperature or nutrients may become more limiting. Average ambient temperatures are known to decline with elevation at an average of 6° C per 1000 m gain in elevation in the Sierra Nevada resulting in a shorter the growing season and a shift in precipitation from a mix of rain and snow at the base of the Lake Tahoe basin to primarily snowfall (Whitney 1979). Major vegetative processes such as photosynthesis, respiration, growth, reproduction, and transpiration are all sensitive to changes in air temperature. As

elevation increases, plants must be able to carry out photosynthesis at progressively lower temperatures and within shorter growing seasons.

Conditions meeting the needs of the greatest number of species occurred at intermediate levels of precipitation, where presumably temperature and soil conditions were also intermediate, and no one of these essential factors was substantially more limiting than another. My results suggest that lower elevation sites with higher precipitation yield the greatest plant diversity, particularly with regard to aquatic, riparian, and meadow associates. Brockway (1998) also found that plant species richness and diversity were lower in association with environmental extremes, precipitation and elevation in particular, and that moisture was most influential on species richness at middle elevations where water availability was more limiting than low temperatures. Gentry (1988) found a similar relationship in Amazonia, where plant species richness increased with precipitation up to 400 cm per year and then reached an asymptote. In my study, plant species richness peaked between 110 and 130 cm/yr, and common species peaked up to 150 cm/yr. These precipitation ranges represent optimum values for plant species richness in the Lake Tahoe basin, and could be used as a trigger for increased consideration of plant species diversity in management activities.

Surprisingly, plant species richness did not decline with elevation, in contrast to many other studies along similar magnitude elevational gradients (e.g., Ogden and Powell 1979, Vasquez and Givnish 1998). For example, Vasquez and Givnish (1998) sampled plant diversity along a 1000 m elevation gradient in a similarly-sized area (139,000 ha) in southwestern Mexico. They encountered a similar total number of plant species (470 plant species) and found a negative relationship between elevation and plant species richness. Vasquez and Givnish (1998) also found that variation in species composition was greater at lower elevations compared to higher elevations (based on Sorensen's index). Like Vasquez and Givnish (1998), Gentry (1988) found a negative relationship between plant species richness and elevation between 1500 and 3000 m in elevation in Amazonia. In the arid and semi-arid southwest, elevational change is believed to be the dominant factor controlling species distribution and composition of riparian plant communities (Szaro 1989, DeBano and Schmidt 1990). However, some studies of plant species richness show no or negative relationships with elevation (e.g., Ogden and Powell 1979). It is likely that the ameliorating influence of aquatic environments on proximate microclimates may be facilitating a higher diversity of plant species at higher elevations than occurs in upland vegetation sites.

Plant species richness per reach may not have declined with elevation, in part, because of unusually high plant diversity associated with subalpine conifer in the Sierra Nevada. Jackson (1985) found that upper elevation vegetation (near tree-line) in the Sierra Nevada had high life-form diversity compared to ecological equivalents in the Cascade, Olympic, or Rocky mountain ranges. The occurrence of high life-form diversity was attributed to the warmer, drier climate of the Sierra Nevada compared to these more northern mountains. It is plausible that this higher life-form diversity translates to higher species diversity than occurs in lower elevation conifer forests, specifically mixed conifer.